The Root Parasitism of Western Australian Santalaceae by **D. A. Herbert,** M. Sc., Department of Biology, University of Queensland.

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The Natural Order Santalaceae is one which is widely distributed over temperate, and to a lesser degree, tropical regions of the earth. In Australia it is represented by eight genera: *Thesium, Santalum, Fusanus, Exocarpus, Choretrum, Leptomeria, Omphacomeria,* and *Anthobolus.* The last four are endemic. All except *Thesium* and *Omphacomeria* have species in Western Australia.

Dr. Diels (1) in speaking of the family says:

> "The Santalaceae also are not confined absolutely to the Eremaea in Western Australia. They surround the South-West province in a narrow margin along the coast, like *Callitris robusta,* for example, or the Myoporaceae. In addition they have enriched the South-west province with some endemic species. Yet the centre of the group is undoubtedly the interior. Many species extend throughout the whole tableland without any big gaps (e.g. *Fusanus spicatus* and *Exocarpus aphylla*) and many are amongst the most common plants of the Western Eremaea."

The Eremaea is that tract of country with an average rainfall of 15-25 cm., and embraces the greater part of the interior of the State. It is true that the order forms a more important part of the formation in the Eremaea than in the moister coastal regions of the South-west but this importance is due to the numbers of the individual plants and their relatively greater size, not to the number of endemic species. They become a conspicuous feature of the vegetation, whereas their specifically more numerous, but smaller allies of the South-west where the vegetation is more luxuriant play an insignificant part in the general picture. A survey of the species in the South-west shows a greater number of species here than in the dry areas. The comparison of the distribution of the Santalaceae with that of the Myoporaceae and *Callitris robusta* is incorrect, as both these are coastal, whereas the Santalaceae are well distributed through the South-west and are continuous with the family on the Eremaea. These other forms mentioned are found both in the Eremaea and on the coast

because the same conditions of dryness occur in both regions, though one is a meteorological and the other a physiological phenomenon.

The root parasitism of several genera of the family is well known, but at the time of the investigation no enquiry had been made into the habits of the Western Australian species except the Sandalwood (2) and the Quandong (3). A brief account of the parasitic habits of the species dealt with in this paper was given in a paper (4) dealing with general characters of phanaerogamic parasites; Mr. Gardner has since examined one of these, *Choretrum lateriflorum*, and a list of its host plants is in press.

Santalum, Thesium, Comandra, and *Osyris* have long been known to derive part of their nourishment from other species. *Santalum album,* the Sandalwood, has been thoroughly investigated by Dr. Barber (5) in India. Other papers, particularly those of Rama Rao, have appeared in "The Indian Forester" with references to Dr. Barber's work and show that this species is an obligatory parasite with a wide range of hosts. Dr. Heinricher (6) of the University of Innsbruck has dealt with *Thesium, Comandra,* and *Osyris* and Dr. Margaret Benson (7) has investigated the habits of *Exocarpus cupressiformis,* an Eastern Australian species.

The last species has a wide range in the Eastern States (including Tasmania) but is only recorded from Western Australia by a doubtful specimen from Wilson's Inlet. The specimens which Dr. Benson investigated were obtained from Killara, New South Wales. The haustoria are very minute and necessitate the use of a hand lens for examination. As the same types of tissue are found in the haustoria of the Santalaceae dealt with later in this paper, Dr. Benson's nomenclature will be adhered to. Three types of haustorium-bearing roots or "necks" were met with:—

(a) A type with irregularly disposed reticulately thickened tracheides as in a *Thesium* haustorium.

(b) A type containing a strand of pitted tracheides with phloem and differing only in the number of protoxylems from the mother root.

(c) A type similar to an ordinary root but lacking phloem.

The haustorium proper consists of two parts, an outer cortical region and an inner conducting region, the "nucleus." The nucleus is shaped like an inverted flask, the neck of the flask towards the host tissue. It consists of an inner hyaline part covered with a layer of lignified cells of the vascular sheath. These form a pad at the end of the flask nearest the neck and connect with the tracheides of the neck. They are termed "phloeo-tracheides" as they differ from typical tracheides in several important par-

ticulars, and combine the structure and function of phloem and xylem. They are lined with protoplasm but contain no nucleus and are reticulately thickened and lignified, but contain no bordered pits as do the reticulately thickened tracheides of the neck.

This paper deals with the parasitism of *Fusanus spicatus.* R.-Br., *Fusanus acuminatus.* R.Br., *Leptomeria preissiana.* DC., *Leptomeria spinosa.* DC., *Choretrum lateriflorum.* R.Br., *Exocarpus aphylla.* R.Br., and *Exocarpus spartea.* R.Br.

THE GENUS FUSANUS.

This genus is limited to Australia. It was adopted by Robert Brown in the Prodromus, and subsequently united by De Candolle with the genus *Santalum.* Bentham and others, however, retain it and the system is followed in this paper.

Three species are known from Western Australia, the Sandalwood (*F. spicatus.* R.Br.) and the two Quandongs (*F. acuminatus* R.Br., and *F. persicarius.* F.v.M.). A fourth, *F. crassifolius,* occurs in the Eastern States.

The leaves of *Fusanus* are broad and the plants are not so characteristically Santalaceous in appearance as those of other Australian genera (except *Santalum*). It would be thought that they would be capable of enabling the plants to lead an independent existence, but examination of two species, *F. spicatus* and *F. acuminatus,* showed that they shared the property of root-parasitism and modified root system known to exist in *Santalum* and other genera already investigated.

PARASITISM OF FUSANUS SPICATUS. R.Br.

Fusanus spicatus. R.Br. (*Santalum cygnorum.* Miquel) is the Western Australian Sandalwood. It produces a scented wood which for burning purposes is equal to that of the Indian Sandalwood (*Santalum album*). Owing to its commercial value the Sandalwood has formed the basis of a considerable industry in the State and, though once extending through the dry interior through the Avon district to the borders of the Darling district, it has now been cut out so thoroughly that it can only be looked for in far back inaccessible districts in any quantity or attaining a good size. Preiss in 1837 collected it round York, where it was known in those days as the "Nut Tree." This name is never heard now. Bentham describes it as a tree of 30 feet, but now it is rare to find it much over 10 or 12 feet. Its regeneration is slow. Unlike *Santalum album,* which reproduces readily from root suckers as well as from seed, it usually reproduces from seed only. Its growth is slow. Trees in the Pingelly plantation showed a maximum height of 10 to 15 feet for over 20 years. It does not produce as much fruit as either *F. acuminatus* or *F.*

persicarius. These factors, combined with the rate at which the Sandalwood was cut out, resulted in the establishment of a sandalwood plantation by the Forestry Department in 1895 at Pingelly, in the Avon District. An area of typical "jam"* country was cleared and planted with sandalwood "nuts." These germinated, grew for a year, and then died. The parasitic habit of the species was not then known. More "nuts" were sown in the virgin bush, and though later the land was taken up for pastoral purposes, the resultant seedlings flourished and have now attained heights varying up to 15 feet. These results are strong indications of the root parasitic habits of the tree. Fires and browsing stock are the main enemies that the plants have to contend with before reaching maturity.

Root System: The Sandalwood produces a branching taproot and a well developed shallow placed lateral root system. These lateral roots vary in size down to about quarter of a line diameter. The smaller roots are very fleshy (Fig. 4) and in section show a large development of cortical tissue. They are very fragile and therefore difficult to trace out, particularly as the species is one which is restricted to hard loamy soils in which it is difficult to dig with a spade. Where the fine roots come into contact with a foreign root they produce a lateral haustorium. In none of the specimens obtained were terminal haustoria found, though these were searched for, as Cannon (8) found them in *Krameria canescens,* (Krameriaceae), an American species, and raised an interesting point in this connection as to the origin of haustoria (see the end of this paper).

The lateral roots may run for a distance of 25 or 30 yards, throwing out smaller roots which form parasitic attachments with foreign roots along their whole length. The range of hosts which one plant may be living on is therefore fairly considerable, both in numbers and in variety. This wide range is shown to an even greater extent by *Nuytsia,* whose underground stem runs for hundreds of yards and whose parasitic attachments may be numbered in thousands along its length.

The depth of these roots in *Fusanus spicatus* is generally not great. As a rule it is about eight inches. They, therefore, might be expected to show some attack on herbs and small shallow rooting shrubs, but at the time of investigation (November) most of the annual vegetation had died with the approach of summer and the smallest shrubs belonged to such species as *Templetonia sulcata* and had a fairly deep rooting habit. These were found to be attacked.

*"Jam" is *Acacia acuminata* and is so called on account of the strong scent of raspberry jam which characterizes the wood.

Host Plants: Rama Rao, in various papers in the "Indian Forester," has recorded the occurrence of haustoria of *Santalum album* on over a hundred species belonging to widely separated genera and families. Among them is an Australian species, the Blue Gum (*Eucalyptus globulus*). Though this number has not been obtained for the Western Australian Sandalwood, it is not improbable that its range is just as wide. In the Pingelly plantation Mr. C. A. Gardner found them on *Acacia acuminata.* At Burracoppin, near the rabbit-proof fence, I obtained them on *Acacia acuminata, Eucalyptus foecunda* var. *loxophleba* and *Templetonia sulcata.* On the goldfields they are parasitic on *Acacia* spp., *Dodonaea lobulata* and *Eremophila* spp. Self-parasitism is fairly common.

The investigation was carried out on specimens obtained at Burracoppin in November, 1920.

Mode of Parasitism (Fig. 1): The fact that Sandalwood is nearly always found growing in very close proximity with another tree, sometimes so close that the trunks are tightly pressed against one another, is very suggestive of a parasitic habit. It is evident that the foreign tree in such cases is the nurse which has enabled the Sandalwood when young to carry on until its roots were able to reach and form parasitic connections with other plants.

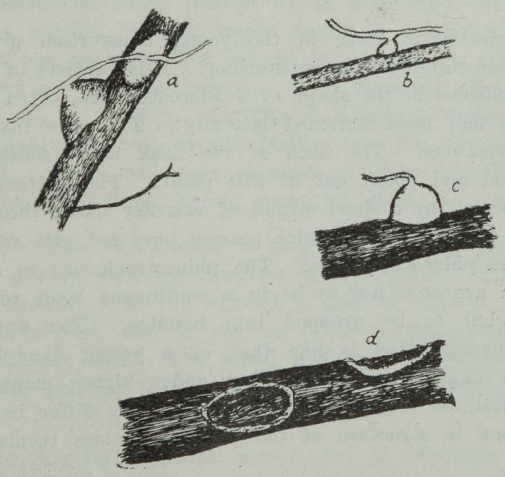

Fig. 1—*Fusanus spicatus*: *a*, haustoria attached to root of *Acacia acuminata*; *b*, young haustorium; *c*, old haustorium with distal portion of parent root shrivelled, leaving an apparently terminal haustorium; *d*, scars on a root of *Acacia acuminata* produced by haustoria which have died and rotted away. (All half natural size.)

The type of haustorium is similar to that of *Santalum*. It arises laterally on a root in contact with another root, either foreign or of the same species. At first it consists of a parenchymatous outgrowth which rapidly enlarges forming a club-shaped organ. The cells in contact with the host have a marked power of destroying and absorbing its tissues, even the outer cork layers. The absorptive cells are rather smaller than the cells of the cortex of the upper part of the haustorium and divide rapidly, pushing in and absorbing the tissues of the cork, cortex, and phloem and even some of the incompletely lignified xylem elements. When the wood is reached the "sinker," as the invading tongue of tissue might be termed from analogy with the absorptive organ of *Viscum* and other Loranthaceae, does not push in any further, but spreads laterally pushing aside the cortex to a certain extent as its margins grow. The cells of the upper part of the haustorium (the part external to the host root) have meantime been dividing and produced a cap-like structure. The whole appearance is like that of a mushroom, the pileus-like part being external to the root and in close contact with it, while the sinker corresponds with the stalk. The inner cells of the external cap have very little power of absorbing the cork layers of the host root with which they are in contact and their function is mainly protective to the sinker, though in *Leptomeria preissiana* they act later as a place for the deposit of waste materials as will be shown later.

The meristematic layer in the young haustorium gives rise to the vascular tissue of the haustorium. This consists of a layer of phloeotracheides in the shape of a Florence flask, often appearing as if it had been flattened laterally. The cells inside this are parenchymatous. The neck of the flask is in contact with the host wood and opens out at this point. The bottom of the flask is connected by a short strand of vascular tissue through the neck to the root. Its tracheides possess bordered pits which are absent in the phloeotracheides. The phloeotracheides in a transverse section are seen not to be in a continuous layer round the parenchyma but to be grouped into bundles. The appearance under low magnification is like that of a young dicotyledonous stem with a number of bundles, but under higher magnification and in longitudinal section it is found that they differ in absence of phloem and in structure of the phloeotracheides themselves.

The host root continues to grow after the haustorial invasion and a callus is formed round the point of entry. This becomes lignified so that in time the bottom end of the sinker is surrounded by wood. The haustoria have only a limited functional existence, the period apparently being about one year. Death and decay occur at the end of this time and a scar, the size varying

with the size of the haustorium, remains. This in time may heal over.

The haustoria are conical and vary up to about three quarters of an inch along their major diameter. They are generally elliptical in section. This is due to the fact that when they have reached the wood, up to which time they are circular in section, further growth in thickness takes place along the line of least resistance, i.e., along the length of the root.

They are produced in large numbers but generally appear to cause little harm to the host, except in the case of a young tree which may be killed by the attack.

These observations indicate that *Fusanus spicatus* is an obligate parasite with a wide range of hosts, and that its haustoria are produced in great numbers, but have only a limited functional existence.

PARASITISM OF FUSANUS ACUMINATUS. R.Br.

Fusanus acuminatus. R.Br., the Quandong, is a small tree attaining a height of about 30 feet. Alternative vernacular names are the Native Peach or the Native Plum, and are in allusion to the fruit which has a red, succulent, edible epicarp with a pleasant acid flavour. Unlike *F. spicatus,* it does not possess a wood of any commercial value (except as an adulterant for consignments of that species, the two woods having a similar appearance) so that it has not been cut out in the forests to any extent. It possesses a very wide range. It is recorded from the Eastern States and in Western Australia is found in similar localities to the Sandalwood, but extends further into the districts of heavier rainfall. Early collectors obtained it from the Kalgan to the Swan and Murchison Rivers, areas in which it is still plentiful.

Like other Santalaceae it does not occur in pure formations, but is always scattered amongst other species. It is frequently found growing close up against a tree of another species, as is the Sandalwood, but is just as often in the open, yards away from another tree. The broad leaf and this apparent isolation, therefore, pointed to a possibility of the quandong being autotrophic.

The investigation was carried out at Merredin in a Gimlet Gum (*Eucalyptus salubris*) forest about six miles from the township, in November, 1920.

Root System: Any doubts as to the possibility of semi-parasitism of the Quandong were removed by digging down and following out the roots. These were found to produce lateral haustoria of a large size and in considerable numbers.

There is a fairly deep taproot as in the Sandalwood, and the lateral roots are very long and extend distances varying up to about twenty yards. It is therefore evident that in cases of apparent isolation of a tree the root may still be long and give rise to haustoria at some considerable distance.

The roots vary in size down to about quarter of a line diameter, the smaller ones being smooth and very pale. There is the typical absence of root hairs common to root-parasitic species. In contact with a foreign root a lateral haustorium of the sandalwood type is produced. Self-parasitism is fairly common.

The haustorium is of the same size and shape as in *F. spicatus* and similar in structure.

Host Plants: The host plants on which haustoria of the Quandong were found were *Templetonia sulcata*, *Acacia acuminata*, and *Eucalyptus foecunda* var. *loxophleba*. These were the only plants close to the trees examined, but in other districts where the Quandong grows they are absent and other hosts should be found. The former two host plants were growing close by the Quandong. Only one specimen showing parasitism on *Eucalyptus foecunda* var. *loxophleba* was found and this was on a long lateral root which was running right under the parasite. It is probable that this root with its lateral branches had been the nurse of the Quandong in its early life.

If, as is probably the case, *Fusanus acuminatus* is an obligate parasite, it must have a very wide range of hosts. At Woodman's Point it is growing amongst a fairly pure stand of *Callitris robusta*, the Native Cypress. In the garden of Forrest House, Perth, there are two trees the only possible host of which is *Pinus pinea*, the Stone Pine, which is four or five yards distant.

THE GENUS LEPTOMERIA.

This genus is limited to Australia, and contains fifteen species, eleven of which are West Australian. *Leptomeria pachyclada*. Diels (in Diels u. Pritzel, Fram. Phyt. Aust. Occ., 178) is the only species described since Bentham's time. The western species do not extend to the Eastern States and vice versa. The plants of the genus are shrubs of a typical Santalaceous appearance with numerous slender leafless branches. The examination of two of these western species, *L. priessiana*. DC., and *L. spinosa*. DC., shows that they are root parasites, but that their modes of attack are very different. Probably all other species have the same habit, but up to the present they have not been examined because of the remoteness from Perth of the localities where they flourish.

PARASITISM OF LEPTOMERIA PREISSIANA. DC.

Leptomeria preissiana is a leafless shrub with slender erect branches, attaining a height of about three feet. It was originally described from Swan River specimens collected by Oldfield and Preiss. Since that time its range has been found to extend far into the Coolgardie district, Diels having collected it at Karalee, a district 268 miles east of Perth on the Great Western Railway. His specimens were similar to the Swan River forms. It is also found on Garden Island. This investigation of its parasitism was carried out on plants growing on the sand plain three miles south of Westonia on the road to Carrabin. This also is in the Coolgardie district, but the typical Avon district forms have not all disappeared with the decreasing rainfall. The species was undoubtedly *Leptomeria preissiana*, but the little lateral racemes of flowers were more terminal than in the Swan River forms.

In the loose, light soil of the Westonia sand plain the plant develops a profusely branched and widely spreading root system. In this it resembles most of the other shrubs associated with it. The texture of the soil is largely responsible, but not wholly Other plants on the heavier loam adjacent are more deep-rooted and their roots do not ramify to the same extent as do those of their neighbours in the sand. Those of *Leptomeria preissiana* are more numerous and more branched; there is a fairly well-developed branched taproot of about three quarters of an inch diameter and the lateral roots vary down to about a quarter of a line diameter. They are pale and fleshy and with the almost total absence of root hairs characteristic of other root parasites. In contact with other roots these small roots give rise to a lateral haustorium. This haustorium in several hundred specimens obtained was never terminal, though in some cases through withering of the distal part of the root it appeared so. It is of the *Fusanus* and *Santalum* type but shows some interesting points not found in these genera.

Owing to the profuseness of the branching of the root system and the sparseness of the surrounding vegetation on the sand plain, it is natural that in their searching after a host the haustoriogenetic roots should come into contact with others of their own kind more frequently than with roots of other species. This is actually the case. Though the haustoria are common on *Acacia signata*, the Wodgil, in thickets of which the plants were growing, by far the greater number were found on the plant's own roots. These are the most convenient to examine, as the *Leptomeria* roots are softer and easier to section than those of *Acacia*, and because of their smooth bark are much neater specimens for preservation. Sections were cut of haustoria attacking both their own roots and those of *Acacia* and the modes of attack found to be similar in all details.

Host Plants: Haustoria were found on *Acacia signata,* the Wodgil; *Duboisia hopwoodii,* the Pituri of the natives (which is here at about its western limit), and commonly on roots of *Leptomeria* itself, as mentioned above.

Mode of Parasitism (Fig. 2): The roots from which the haustoria arise are generally about a quarter of a line in diameter. They are white and fleshy and as in the case of the sandalwood the greater part of the area in section is occupied by large-celled cortical tissue, the vascular tissue occupying a small central strand. On this account they are rather brittle, but not nearly so difficult to remove from the ground on this account as are those of *Nuytsia floribunda.* When they come in contact with a host root a haustorium is formed laterally. This at first consists of a clavate mass of parenchymatous tissue with a meristematic zone continuous with the vascular elements of the root. The cork

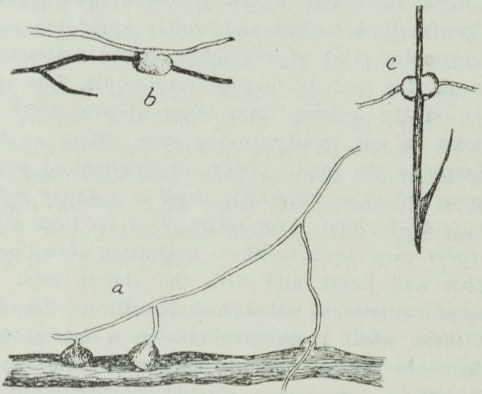

Fig. 2—Haustoria of *Leptomeria preissiana*: *a,* typical form; *b* and *c,* examples where the cap has wrapped round the small host roots to produce a structure somewhat similar in outward appearance to the haustoriogen of *Nuytsia floribunda.*

cells of the host are first attacked and absorbed. The absorptive cells are smaller than those of the upper part of the young haustorium. Subsequent development is similar to that found in *Fusanus spicatus* and in *Fusanus acuminatus.*

The phloeotracheides are reticulately thickened and as in *Exocarpus* differ from the tracheides of the neck in absence of circular bordered pits. They are accompanied by unthickened protoplasmic nucleated cells of similar size and shape which are scattered amongst them. The inner part of the "nucleus" of the haustorium is occupied by parenchymatous cells.

Morphology of the Haustoria of Leptomeria preissiana: In the beginning of the attack the haustorium is a small clavate body of little over half a line in diameter and consisting chiefly of parenchymatous tissue. This rapidly enlarges as the sucker penetrates the cork and the underlying tissues and the size it attains depends mainly on the size of the root attacked.

A small root, say a line in diameter, may be almost completely wrapped round by the cap portion of the haustorium in which case the appearance is very like the haustoriogen of *Nuytsia floribunda* (9). In *Nuytsia* no tongue of vascular tissue is intruded into the host root. The absorbing organ forms a complete circle round the root it is attacking and on the inside by rapid division of the cortical cells small tongues of parenchymatous assimilatory tissue are developed. *Leptomeria* differs in having a distinct sinker with vascular tissue, and the wrapping round of the cap portion of the haustoria on small roots does not result in a fusion on the far side and production of a ring. The ring in *Nuytsia* has been termed the haustoriogen on account of the production of these assimilatory tongues on its inner surface. These are not found on the inner side of the cap of *Leptomeria preissiana.*

If the host root is of sufficient size the *Leptomeria* haustorium will attain a diameter of about one third of an inch when fully developed. It may be circular or elliptical when looked at in face view, and is conical when looked at from the side and is up to one third of an inch in height.

Whether the haustorial cap is circular or elliptical in face view depends on the amount of penetration of the sinker. Up to the time that this reaches the wood, it is circular. When, however, it reaches this and starts to spread out it finds that the path of least resistance is along the vertical length of the host root and it commences to grow in this direction. The cap grows at the same time in the same direction and becomes elliptical in section.

The haustoria are produced in great numbers. Each plant examined had produced several hundred and probably the number ran into thousands. The amount of food material obtained must be very considerable, and may account for the luxuriant development of flowers.

Developments of the Haustoria after attaining maturity: When the haustoria have attained this size growth ceases. The host root continues to grow and the edges of the sinker become embedded in newly formed wood. Callus tissue is produced in the inner cortex, and wood elements appear here also. The cap begins to be forced outwards, and the appearance is as if the

plant is endeavouring to strangle the invading tissue. The haustorium then commences to die. Its cortical cells are now used as a place for the deposition of waste products. Calcium oxalate, which occurs in other parts of the plant to a very limited extent, is deposited in large sphaero-crystals. The connecting root shrivels, dries, and turns black, and the cortical tissues shrivel and disintegrate. Finally the only evidence of attack is a deep scar on the host root with the remains of the vascular tissue of the haustorium still protruding. The scar generally heals up in time leaving a longitudinal depression varying in size according to the size of the original injury.

Haustoria are formed at all times of the year. On a single root several may sometimes be found in all stages from the small parenchymatous outgrowth up to the withering haustorium of a third of an inch diameter. Their limited functional existence is, therefore, not dependent on the seasons.

PARASITISM OF LEPTOMERIA SPINOSA. DC.

Leptomeria spinosa is a much branched rigid but somewhat decumbent shrub of about two feet in height, and like the other members of its genus leafless at the time of flowering (September to November). Like *Leptomeria preissiana* it has a wide range, Drumond, Preiss, Oldfield, Maxwell and others having collected it in the Darling, Avon, Stirling, and Warren districts. The plants on which this investigation was carried out were growing on a sand plain* near Yoting in the Avon district. (Yoting is an agricultural district 135 miles from Perth by railway, on the York to Merredin line.)

Root System: The plant develops a well branched root system of a type similar to that of *L. preissiana*. There are the typical pale, somewhat fleshy roots with the almost complete absence of root hairs. These ramify through the loose sand, but unlike the other species, when they strike a foreign root do not always produce haustoria. The only species which they were found to be attacking was *Eremaea pilosa*, a low Myrtaceous shrub fairly widely distributed through the dry areas. The first plants of *Leptomeria spinosa* examined were growing amongst a thicket of native cypress (*Actinostrobus acuminatus*) with here and there a shrub of the grotesque-fruited *Hakea platysperma* and other species. The roots of these were examined but in no case were

* This sand plain was characterized by a very glaucous form of *Gastrolobium spinosum* with thick entire leaves. Transitions of the normal form with rather thin leaves with lateral spines were found so that it could not be regarded as a distinct variety.

haustoria found. On *Eremaea*, however, they were exceedingly numerous. The species was not very common on this sand plain and all the plants observed were growing close to the base of *Eremaea* shrubs. Self-parasitism was not observed. In *L. preissiana* it was the most noticeable characteristic. It is therefore evident that *Leptomeria spinosa* possesses a higher degree of specialisation in its selection of a host than its relative and the other species examined. It probably has other hosts as it has a very wide range, though *Eremaea* and other allied Myrtaceae have the same range, but does not share in the apparent indifference to the nature of the host root shown by the Loranthaceous *Nuytsia* and (to a lesser extent) *Fusanus* and *Exocarpus*.

Mode of Parasitism: The roots vary in diameter down to about a quarter of a line in diameter. They are ultimately more slender than those of *L. preissiana*. When one of these small roots comes into contact with a host root it applies itself closely to it. What appears at first sight to be a terminal haustorium is formed, but close examination shows that it is really lateral but very close to the tip of the root. The tip grows on and the root creeps along the host root producing small haustoria at intervals of about one line under ordinary circumstances (Fig. 5). The haustoria are not produced on the same side of the root. Some are produced on the side in contact with the host root, others on the sides, and others on the side remote from the point of contact. These latter, however, turn round and apply themselves to the host in the ordinary way. The only difference is in the length of the neck.

One root creeping along may produce thirty or forty haustoria. Though in close contact there is no fusion between the cells of the host and parasitic roots. This can be shown where a root has crept along and worked its way into a fissure in the bark of the host root. It forces its way through the living bark but emerges without having produced more than a mechanical piercing. *Cuperus rotundus*, the Nut Grass, one of the native Cyperaceae, which is a common weed of cultivation, does this and at Spearwood (a few miles south of Fremantle) often damages onions and potatoes in the same way with its creeping rhizomes. All the parasitism of *Leptomeria spinosa* is done by the haustoria and never by the root itself.

Morphology and Histology of the Haustoria: The haustoria as in *Leptomeria preissiana* are lateral. They first appear as a parenchymatous outgrowth and if on the side of the root in contact with the root, they grow downwards absorbing the cork cells and penetrating the cortex. The shape is similar to that of the other species. If they are formed on the other side of the

root the length of the neck is much greater and the shape of the whole clavate instead of conical. From a meristem the vascular system of phloeotracheides is produced and is of the shape of an inverted flask connected with the tracheides of the neck at the bottom and having the top near the region where the end of the haustorium is in contact with the cortical cells of the host. The ends of the phloeotracheides are not in contact with the cells of the foreign root; the actual attack is carried out by unlignified parenchyma cells.

The haustorium does not penetrate as far as the wood. In the great majority of cases it does not go far into the cortex, and

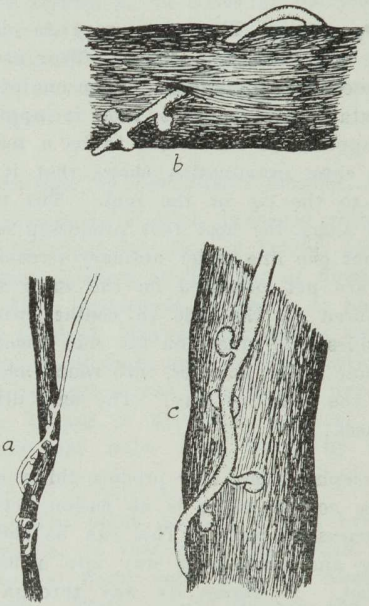

Fig. 3—Haustoria of *Leptomeria spinosa*: *a*, half natural size; *b*, mechanical piercing of the bark of *Eremaea pilosa* by root of *L. spinosa*, enlarged; *c*, haustoria arising from a root of *L. spinosa*, enlarged.

the root can be removed with the haustoria intact by pulling it gently away from the host. The same factors which tend to make the haustorium of *L. preissiana* elliptical in section are, therefore, not operating and the section in this species is circular. The maximum size is about a line and a half in diameter and two lines long.

The number produced is very great and amounts to several thousands for each plant. In November, when they were collected,

all stages of development were found, which would seem to show that they are formed all the year round.

Their functional existence is not limited except by the life of the root. Examination of several hundred showed that only where the parent root had died off had the haustoria died.

The fact that plants belonging to this species were not common in spite of the abundant production of seed, and that in all the cases examined they were parasitising the same species of host indicates that not only is *Leptomeria spinosa* an obligate parasite, but that its choice of hosts is very restricted.

THE GENUS CHORETRUM.

The genus *Choretrum* is limited to Australia, and contains five species, three of which are found in Western Australia. These are *C. glomeratum.* R.Br., *C. pendulum* Tovey and Morris, and *C. lateriflorum.* R.Br. The plants of the genus are shrubs with slender rigid branches with the leaves all reduced to minute scales, which are usually deciduous.

Parasitism of Choretrum lateriflorum. R. Br.:

Choretrum lateriflorum is a shrub of two or three feet with erect broom-like branches. It occurs round King George's Sound in the Warren district in Western Australia and has a wide range in Victoria and New South Wales. At Denmark it grows in the Karri (*Eucalyptus diversicolor*) forest in hilly country. At Albany it grows on sand plain amongst Jarrah and Sheoke, and at Redmond in low lying, sandy, swamp country. The investigation of its parasitism was carried out at Redmond, near Albany, in March, 1921.

Host Plants: Haustorial attachments were found on *Casuarina fraseriana,* one of the sheokes, and also on a species of *Pimelea* in large numbers. Self parasitism is also common. Other roots not belonging to these species were found attacked but it was not certain which plants they belonged to.

Root System: *Choretrum lateriflorum* has a well developed lateral root system, the roots being reddish-brown and the smaller rootlets white. The small haustorium-bearing rootlets are extremely slender and fragile, some being about the diameter of a hair, others varying up to about an eighth of a line. When they come into contact with a root they creep along it giving rise to lateral haustoria along their length.

The Haustoria (Fig. 4): The haustoria are very minute and either discoid or conical in shape. When full grown they do

not exceed about one third of a line in diameter at the point of attachment, and most of them are only half this size. Because of their small size and the minuteness of the root on which they are borne it is not to be expected that they will penetrate far into the host. In section it is found that though their attack is well marked they do not go far into the cortex and do not reach the wood. The actual task of attacking and dissolving the cells of the foreign root is undertaken by parenchymatous cells at the tip, the phloeotracheides not being in contact with the host tissue. No small roots were found attacked by *Choretrum* haustoria. It is probable in such a case that the sinker would pene-

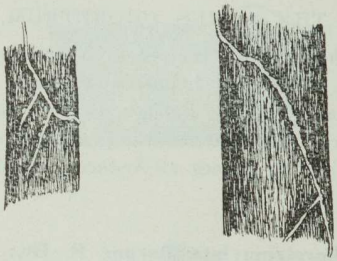

Fig. 4—Haustoria of *Choretrum lateriflorum*, half natural size.

trate as far as the wood, as the structure of the haustorium attacking a large root is very similar to that of the haustoria of *Leptomeria preissiana* and *Fusanus* in their young stages.

Haustoria are probably formed at all periods of the year. These were collected in March, at the end of a long dry summer, and some were within about four inches of the surface of the ground. There was no evidence of limited functional existence as in *Fusanus* and *Leptomeria preissiana*.

In a few cases they appeared terminal but under the microscope it was clear that they were lateral but that the root had died back, giving them a terminal appearance. In other examples the hair-like rootlet of *Choretrum* crept along the host root and to the naked eye appeared as if it were fusing with it along its lower surface, i.e., as if the cortical cells were capable of absorbing the cork layer. On sectioning, however, it was found that the points of contact represented immature haustoria.

THE GENUS EXOCARPUS.

Eight species of *Exocarpus* are recorded from Australia, and three of these are known with certainty to occur in extra-tropical Western Australia. These are *E. odorata* (restricted to this State),

E. aphylla, and *E. spartea*.. A fourth species common in the Eastern States is recorded from the evidence of a doubtful specimen of *E. cupressiformis* from Wilson's Inlet collected by Oldfield. *E. latifolia* from the north of the State, has been found by Gardner (10) to be parasitic on *Petalostigma*, *Canthium*, *Terminalia*, and *Callitris intratropica*; its haustoria are described as slug-shaped, about 2cm. long and 1.5 cm. wide, thick and fleshy, numerous.

Parasitism of Exocarpus aphylla:

Exocarpus aphylla, a shrub of 3 to 8 feet, occurs in the Eremaea and is easily distinguished amongst the other vegetation by its leafless, hard, thorn-like branches. It prefers loam soil and on the wheat belt is found in Salmon Gum (*Eucalyptus salmonophloia*) and Gimlet Gum (*Eucalyptus salubris*) forests. It has a deep root system and the stony loam in which it grows renders it very difficult to investigate its root system. Only one plant was examined. This was at Burracoppin, a district forty miles east of Merredin and near the edge of the wheat belt.

One shrivelled haustorium was found on an *Acacia* root and on the same root were scars, the records of an old attack from which the plant had recovered. This haustorium was too withered to section, but was of the same type as those produced by *Leptomeria spinosa*, *Fusanus*, *Santalum*, and other genera. It measured about one quarter of an inch in diameter at the point of contact with the host root, so that it compares in size with those produced by *E. spartea*, described below. Those of *E. cupressiformis*, of which a full account is given in Dr. Benson's paper, are very minute and compare with those of *Choretrum lateriflorum* R.Br., which are also described above.

The habit of *Exocarpus aphylla* is suggestive of parasitism. The leafless branches, its insignificant flowers, and the fact that it grows up close to other plants (sometimes appearing to grow out of the centre of another shrub) point to this. Unfortunately the time available to investigate it was very short. The investigation was carried out late in the afternoon on plants about forty miles from Merredin, which had to be reached by nightfall, and the cement-like nature of the soil and the deep rooting habits combined against the obtaining of more evidence.

Exocarpus aphylla is, therefore, parasitic on at least one host, and its haustoria are of the *Santalum* type. Further investigation is necessary to determine whether, like *Leptomeria spinosa*, it is restricted in its choice of hosts, whether it is an obligatory parasite, whether it ever has self-parasitic habits, and if haustoria are produced at any particular season or throughout the year. The shrivelled haustorium obtained was in the hard-baked dry soil

about six inches below the surface. Here, of course, none would be formed in summer, so that their production would be seasonal in the upper layers. Down below, however, where moisture is available throughout the year, it is possible that they are being formed at all seasons.

Parasitism of Exocarpus spartea. R. Br.:

Exocarpus spartea R.Br., like *E. Aphylla*, has a wide range through the Eastern States, as well as through the West. It is very variable in habit. Specimens obtained from Geraldton in November, 1919, were from a low shrub of about 4 feet in height, similar to the form found round Perth. This is the form found in sandy soil. In the loam at Northam and Greenhills the species takes the form of a tall shrub, or small tree, of about 15 feet with slender rather pendulous branches. These were flowering in November, 1920. The Geraldton plants were in an advanced stage of fruiting at this time, but this is natural as the season becomes later as you go south.

The species is recorded from King George's Sound in the south to the Murchison River in the north. In the east Gardner has collected it at Wyalkatchem, Kellerberrin, Kondinin and Esperance. The investigation of its parasitism was carried out at Greenhills in November, 1920. Here it was growing amongst York Gum (*Eucalyptus loxophleba*) and Jam (*Acacia acuminata*), the two species that comprise the characteristic arborescent vegetation of the Avon district. In April, 1921, plants were examined at Nedlands on the Swan River, a few miles from Perth. Here they were growing in sand in an open Jarrah (*Eucalyptus marginata*) forest, with a number of small shrubs round their bases.

Host Plants: The soil at Greenhills was a red, sandy loam and supported a vegetation consisting of herbaceous Compositae (*Helichrysum* spp., *Brachycome* spp. etc.), a few grasses, and the two trees already mentioned. Here and there were a few sheokes (*Casuarina glauca*) and Flooded Gums (*Eucalyptus rudis*) but no Exocarpus trees were growing near them. Haustoria were obtained at a depth of about eight inches on both *Eucalyptus loxophleba* and *Acacia acuminata*.

At Nedlands the flora was quite different. There were over a hundred different species of trees and shrubs growing in the area. Where the *Exocarpus* shrubs were growing were *Gompholobium tomentosum, Casuarina humilis, Banksia menziesii*, and *Banksia ilicifolia*. Parasitic attachments were found on all these species, and self-parasitism was common.

Root System: The roots of *Exocarpus spartea* are similar to those of the other species described. They are reddish-brown in colour, the smaller ones being pale and whitish, with a characteristic lack of root hairs. There is a branched taproot with a large number of ramifying shallowly placed lateral roots. At Greenhills, in the loam, these came to within six inches of the surface; in the Nedlands sand they were about three inches down.

The Haustorium (Fig. 5): The presence of another root is not necessary for the production of haustoria, though they are formed more abundantly if one is there. They arise laterally as small parenchymatous nodules which enlarge by rapid division of an apical meristem. Where no host root is present they ultimately reach a length of about two lines and a breadth of about one line at the broadest part. The shape is clavate, the neck end being the narrower. The structure follows the same lines as in *Leptomeria spinosa.* The vascular tissue is in the shape of a flask but the part corresponding to the neck of the flask is much longer than in the case of any of the other species examined and is often much broader. Its phloeotracheides end in the cortical tissue of the tip, the actual attack being carried out by parenchyma cells. This vascular sheath, like the other species, has its phloeotracheides grouped into bundles similar to the arrangement in a young stem, but differing in their microscopic structure. The bundles are more widely separated, however, than in the other species and in a longitudinal section one side or the sheath may be missing owing to the section having passed between two of them instead of through them. In haustoria not connected with a host root the vascular sheath may not be flask-shaped, but may round parallel with the outer surface of the haustorium.

When the young haustorium is formed in contact with another root, either one of its own species or a foreign one, its mode of attack is similar to that of *Leptomeria spinosa,* but is much more feeble. If it is in close contact it may penetrate into the cortical tissues dissolving the cork layer and the outer cortical layers. The host wood is not reached. All the collecting of food materials from the host cortex is done by parenchymatous cells. If the haustorium is not in close contact with the root, there may be no piercing of the tissue at all. The haustorium may run along the root like an ordinary root, and the only fusion take place along its sides and not at the tip. Such a fusion is very weak and the haustorium readily comes away at a very light pull.

An interesting case was where a haustorium had come into contact with the wood of a root of *Acacia acuminata* which was

exposed through a splitting of the bark. The haustorium had run along between the wood and bark, fusing with the latter, but showing no signs of attempting to attack the wood (Fig. 5 *d* and *e*).

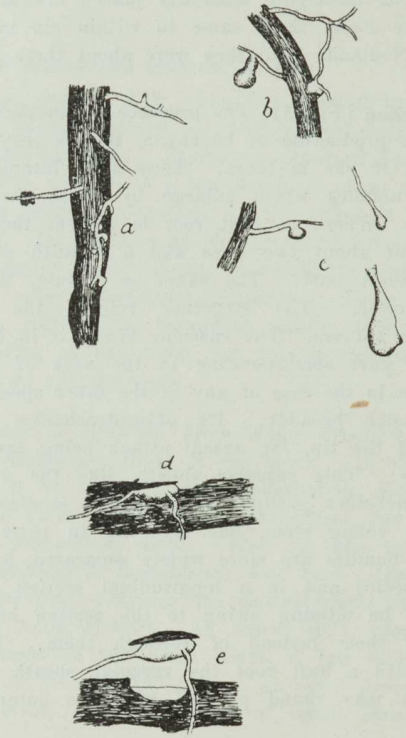

Fig. 5—Haustoria of *Exocarpus spartea*: *a*, root, half natural size, producing haustoria in contact with a root of *Gompholobium tomentosum*; *b*, an *Exocarpus spartea* root with one haustorium arising independently of a host, the other attacking its parent root; *c*, independently formed haustoria showing their lateral nature; *d*, a haustorium formed in a fissure in the bark and adhering to the bark on the lower side; *e*, same haustorium raised to show that it did not attack the wood of the host.

GENERAL FEATURES OF PARASITISM OF THE SANTALACEAE.

Self Parasitism: Self-parasitism is common in five of the seven species examined, and it is not improbable that the other two possess the same property. One would not expect it to be

a very successful operation, for a necessary condition for parasitism is that the parasite should have a higher osmotic power than its host. Thus McDougal (11) in the artificial production of parasitic conditions was able to make *Cissus* with an osmotic activity of 11.34 atmospheres maintain itself on *Opuntia blakeana* at 8.88 atmospheres. The osmotic pressures of the cells of the haustorium and of the root cells of the same plant might be expected to be so close that attempts at self-parasitism would be unsuccessful. The work of Hill (12) and others, however, indicate that the success with which such an attempt is met with in the cases described may be accounted for by differentiation in osmotic pressure in the haustorium. Working on the root hairs of salt marsh plants Hill showed that in contact with a higher concentration of solution than in their own cells they automatically increased their osmotic activity.

The Haustoria: Gautier has shown in the case of *Melampyrum pratense,* and Barber in the case of *Santalum album,* that the haustoria always arise laterally. Goebel, on the strength of their lateral nature in the known cases, advanced the theory that they were distinct organs, and did not arise as modifications of roots. Cannon, however, in his work on *Krameria canescens* (Krameriaceae) showed that though in this species lateral haustoria were formed they were also produced terminally as modified root tips, and are, therefore, not new organs. "In older plants, however, the haustoria may be new organs, but this is not proved."

In none of the seven species described above were there any terminal haustoria. In a few cases in *Exocarpus spartea* (Fig. 7) and in *Leptomeria preissiana,* what appeared at first sight to be terminal organs were found, but if the real lateral nature could not be discerned by examination with a lens, it was found on sectioning and examination under the microscope. In *Fusanus spicatus, F. acuminatus, Leptomeria preissiana, L. spinosa,* and *Exocarpus spartea,* old haustoria were met with having a terminal appearance, but this was due to the root having died back to the point where the haustorium had arisen.

The phenomenon noticed in *Exocarpus spartea* (Fig. 7) the fact that the phloeotracheide sheath of a haustorium not in contact with a host runs parallel with the outer surface of the organ, seems to show that the flask shape of this sheath is directly due to the entry into the host. When the haustorium is young the first formed phloeotracheides are parallel to the surface (that is at the "bottom of the flask"). When the host bark has been pierced, however, the vascular elements are produced from a meristem following behind this first point of entry and the result is a narrowing to the flask shape.

The nature of the haustoria does not seem to be a generic character. Those of *Leptomeria preissiana* are similar in structure to those of the two species of *Fusanus*, differing only in size. *Leptomeria spinosa* differs in quite a marked manner in size and appearance, and do not penetrate to the same extent as the other member of the genus. They resemble more those of *Choretrum lateriflorum* and *Exocarpus spartea*, the main differences of which lie in their size. This *Exocarpus* differs from *E. cupressiformis*, as described by Dr. Benson, in that its haustoria, though attaining a considerable size do not penetrate further than the outer cortical layers of the host. Thus it appears that the general type is the same throughout the genera, but that though it varies greatly in the different species the differences are not generic.

SUMMARY.

1. The seven Santalaceous species examined, *Fusanus spicatus*, *F. acuminatus*, *Leptomeria preissiana*, *L. spinosa*, *Choretrum lateriflorum*, *Exocarpus aphylla*, and *E. spartea* are all root parasitic, but differ in mode of attack.

2. In the first three species there is contact between the vascular system of the haustorium and that of the host root. In the others (except *Exocarpus aphylla*, of which the material obtained was not sufficient for a thorough examination), the attack was carried out by parenchymatous cells which only penetrated into the cortex; the phloeotracheides were not in contact with host tissue.

3. *Fusanus spicatus* is an obligate parasite and from the large numbers of haustoria found in all the plants of other species examined, they probably share this property.

4. *Leptomeria spinosa* shows discrimination in choice of a host. At Yoting it was only found on *Eremaea pilosa*. The other species are more cosmopolitan in taste.

5. In *Exocarpus spartea* the presence of a host plant is not a necessary preliminary to haustorium formation.

6. The haustoria in all cases are lateral and appear to be distinct organs and not, as is sometimes the case with *Krameria*, modified root tips.

7. In *Leptomeria spinosa* the roots sometimes pierce the outer cortical layers, but there is no fusion with them by the ordinary roots. All absorption is done by haustoria.

8. The flask shape of the vascular sheath of the haustoria

of these species is ascribed to the method of attack on host plants. This is not produced in haustoria of *Exocarpus spartea* formed independently of a host root.

9. The phloeotracheides in these species occur in bundles round an inner parenchymatous core, and not in a continuous layer, as in *Exocarpus cupressiformis*, nor in two bundles as in *Thesium*.

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